Quantitative Genetics of Inbreeding in a Synthetic Maize Population

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ABSTRACT

The average effects of inbreeding depression have been measured extensively in maize (*Zea mays* L.), but the influence of inbreeding on genetic variance has not been well studied. Two hundred random S_1, S_2, S_3, and S_4 lines were developed from the BS13(S)C0 population by single-seed descent and a set of 200 related half-sib families were developed from the S_1 lines. The lines and half-sib families were evaluated in replicated yield trials for six agronomic characters. Under a purely additive model, the expected variance among inbred individuals is exactly twice the variance of noninbred individuals. The observed variance of inbred individuals in our study was 1.18 times the variance of noninbred individuals or less for five of six traits studied. By contrast, variance of dominance deviations of inbred individuals ranged from 1.6 to 3.3 times the variance of dominance deviations of noninbred individuals for five of six traits studied. A negative covariance between dominance deviations and breeding values in inbred individuals was found for all six traits. An estimator of the degree of dominance for arbitrary allele frequencies was developed. The estimated average degree of dominance in BS13(S)C0 ranged from 1.28 to 2.76, corresponding to overdominance or pseudo-overdominance. Our results suggested that some regions of linked genes have large effects on inbreeding depression in this population.

Inbreeding depression in maize is a ubiquitous phenomenon found in all populations and for most measurable traits. Significant inbreeding depression was found for 19 of 22 phenotypic and agronomic characters evaluated in six agronomic studies of inbreeding in maize (Benson and Hallauer, 1994; Cornelius and Dudley, 1974; Good and Hallauer, 1977; Hallauer and Sears, 1973; San Vicente and Hallauer, 1993; Walters et al., 1991). All of these studies found the decrease in population means with inbreeding was a linear function of the inbreeding coefficient. Linear regression on the inbreeding coefficient accounted for 98% or more of the variation among inbred generations for grain yield and 90% or more of the variation among generation means for all traits other than grain yield. Non linearity of changes in population means in the inbreeding coefficient is a function of epistatic gene action (Crow and Kimura, 1970, p. 80; Kempthorne, 1957).

Average effects of inbreeding in maize, i.e., changes in the population mean with inbreeding, are well understood. However, studies of changes in genetic variance with inbreeding have been rare. Studies of changes in genetic values of independent lines with inbreeding have revealed large variability among lines (Bartual and Hallauer, 1976; Cornelius and Dudley, 1974, 1976; Obilana and Hallauer, 1974) and variability in inbreeding depression (Sing et. al., 1967). However, with the exception of Cornelius and Dudley (1974, 1976), variability attributable to inbreeding in these studies could not be described in terms of any quantitative genetic effects. Cornelius and Dudley (1974, 1976) and Coors (1988) provided some quantitative genetic analysis of the effects of inbreeding on genetic variability in maize. Both studies found that dominance deviations of inbred individuals became negatively correlated with their breeding values, whereas dominance deviations and breeding values are independent in noninbred individuals by definition. This finding provides some insight into how inbreeding affects inheritance of quantitative traits, but clearly better insights would be useful. The work of Cornelius and Dudley (1974, 1976) and Coors (1988) did not permit much additional information. Coors (1988) had only a single generation of inbreeding which limited the number of estimable quantitative genetic parameters. Cornelius and Dudley's (1974, 1976) mating design was inadequate to resolve all of the desired genetic effects (Cornelius, 1988). Shaw et al. (1998) evaluated five traits in a natural population of *Nemophila menziesii* Hook. & Arn. and also found a trend towards negative association between breeding values and dominance deviations in inbred individuals, although none of the covariance estimates were significantly less than zero. In addition to the negative association with breeding values, Shaw et al. (1988) found that dominance deviations of inbred individuals were numerically (no hypothesis test available) larger in magnitude than dominance deviations of noninbred individuals for four out of five traits. Gallais (1984) concluded in a study of inbreeding and crossing in alfalfa that nonadditivity was more important in inbred relatives than it appeared to be in noninbred relatives. The study of Gallais (1984) did not address specific quantitative genetic components to the degree of other studies.

Genetic effects of interest to breeders, namely breeding values and dominance deviations of individuals, are functions of the action of alleles at individual loci. In particular, inbreeding depression is an outcome of directional dominance, which the historical literature in maize has shown to be quite important. Estimates of the degree of dominance of genes affecting quantitative traits have nearly always been greater than one, corresponding to overdominance, in biparental F_2 populations (Gardner et al., 1953; Gardner and Lonnquist, 1959; Han and Hallauer, 1989; Moll et al., 1964; Robinson et al., 1949). Random mating of F_2 populations to reduce linkage disequilibrium, however, generally has reduced the estimate of the degree of dominance to approximately one or less, corresponding to partial or complete dominance (Gardner and Lonnquist, 1959; Han and Hallauer, 1989; Moll et al., 1964).

The objectives of our study were to dissect genetically

the effects of inbreeding in the BS13(S)C0 maize population in terms of a single-locus genetic model for inbred relatives by obtaining estimates for genotypic covariance components for inbred relatives, σ_A^2, σ_D^2, D_1, D_2^*, and H^*. In particular, the following questions were asked: (i) How does inbreeding affect the total genetic variance among individuals? (ii) How does inbreeding affect the expression of dominance deviations? (iii) How does inbreeding affect the relationship between dominance deviations and breeding values? (iv) What is the estimated average degree of dominance in BS13(S)C0? A secondary objective was to develop improved hypotheses to explain a perceived lack of response to S_2-progeny recurrent selection in BS13(S)C0.

MATERIALS AND METHODS

Choice of Population

The BS13(S)C0 population was chosen for this study because of the perceived lack of response in population per se performance to S_2-progeny recurrent selection. BS13(S)C0 is a derivative of the Iowa Stiff Stalk Synthetic maize population which was formed in 1933 and 1934 by Dr G. F. Sprague (Lamkey et al., 1991). The original stiff stalk population (BSSS) was subjected to seven cycles of half-sib recurrent selection with the double cross Ia13 used as a tester. After seven cycles of half-sib selection, the resulting population, BSSS(HT)C7, was sampled to form the BS13(S)C0 population (Lamkey et al., 1991). The BS13(S)C0 population was subjected to eight cycles of S_2 and S_1 recurrent selection (S_2 remnant seed was recombined in all except Cycles 3 through 5, in which S_1 remnant seed was recombined; Lamkey et al., 1991). No significant improvement in per se performance was found from inbred progeny (S_2 and S_1) selection in BS13(S)C0 in evaluations of the first four cycles of selection by Helms et al. (1989) or the first six cycles of selection by Lamkey (1992). Given response patterns observed in other selection programs in BSSS, Lamkey (1992) concluded that selection response was expected. Inadequate genetic variation, overdominance, and genetic drift were provided as possible explanations for the lack of response in BS13(S)C0 (Lamkey, 1992).

Mating Design

The mating design for this study was chosen on the basis of considerations for studying inbreeding given by Lynch (1988) and Cornelius and Van Sanford (1988). Most importantly, a design was needed with (i) a large range in inbreeding coefficients, (ii) inbred lines developed with the maximum rate of inbreeding, i.e., the largest attainable inbreeding coefficient in the smallest number of generations, and (iii) noninbred relatives related by coancestry with the inbred relatives under study.

We developed 229 random inbred lines by single-seed descent from the BS13(S)C0 population. Inbreeding was initiated in the summer of 1993 by randomly choosing 229 individuals and self pollinating them. In each subsequent generation of inbreeding, the 229 lines were planted ear to row and the first three plants of each row were self-pollinated. A single ear (i.e., a single plant) from each line was randomly chosen to advance the line. Adequate quantities of seed for yield trials were obtained by sib-mating within inbred generations of each line. A single row of 20 plants of each generation of each line was planted and sib-mated. The first three generations of inbreeding, S_1, S_2, and S_3, were sib-mated in 1995 and the S_4 was sib-mated in the 1995-1996 winter nursery. Sib matings were conducted in which each plant was used once as male and once as female and reciprocal crosses within rows were excluded, i.e., plants were not crossed to the same sib as both male and female. Seed from all successful pollinations in a row was harvested and bulked. Half-sib families were developed by planting and detasseling a single row of 15 plants of each S_1 line in isolation with the base population, BS13(S)C0, as a male pollinator in the 1995 summer nursery. Seed from all plants harvested within a single row was bulked to form a half-sib family.

The BS13(S)C0 population segregates for *hm1*, a single gene that confers susceptibility to Northern leaf spot [caused by race 1 of *Bipolaris zeicola* (Stout) Shoemaker (teleomorph = *Cochliobolus carbonum* Nelson)]. An epidemic occurred during seed increase in the 1995 summer nursery. Each line in each generation of inbreeding was scored for its reaction to the disease to determine the genotype of the self-pollinated parent of the line. Twenty-seven of the 229 noninbred founder individuals were inferred to be homozygous for the allele conferring susceptibility and were discarded. Two additional lines that became fixed for the allele conferring susceptibility in the S_2 generation were dropped as well, reducing the total number of lines for evaluation to 200. A χ^2 test (data not shown) revealed no significant deviation from Hardy-Weinberg proportions at this locus. We assumed that variation for disease reaction was not genetically correlated with quantitative traits because we found Hardy-Weinberg proportions and because little selection against this gene has occurred during selection programs in BSSS, from which BS13(S)C0 was developed.

Experimental Design

The 200 inbred lines in four generations of inbreeding and the half-sib families developed in isolation were planted in replicated yield trials at three locations near Ames, Carroll, and Fairfield, IA, in 1996 and 1997. The Fairfield 1996 location was discarded because of flooding. The experimental design was a split-plot with inbreeding levels as whole plots and individual lines within inbreeding levels as subplots. Whole plots were arranged in a randomized complete block design. Subplots were arranged in 10 by 20 row-column lattice [$\alpha(0,1)$] layouts with each inbreeding level in each environment representing its own, independent two-replicate lattice.

In addition to evaluating all 200 lines individually, balanced bulks were made with an equal number of kernels of each of the 200 lines for each level of inbreeding. These five bulks, along with a balanced bulk collected from approximately 100 ears harvested from the male pollinator in our 1995 isolation, were planted in a bulk entry experiment to measure inbreeding depression. Five replicates were planted in each environment in a randomized complete block design.

All plots were standard two-row yield plots, 5.49 m in length, with 0.76 m between rows. Plots were machine planted at 76 510 plants ha^{-1}, and thinned to 62 165 plants ha^{-1}. Data were collected on grain yield (Mg ha^{-1}) adjusted to 15.5 g hg^{-1} grain moisture, grain moisture (g hg^{-1}), ear height (cm), plant height (cm), days to mid pollen (days after June 30 until 50% of the plants in a plot were shedding pollen), and days to mid silk (days after June 30 until 50% of the plants in a plot had visible silks extruded).

Seed for both experiments was treated with carboxin (5,6-dihydro-2-methyl-*N*-phenyl-1,4-oxathiin-3-carboxamide) and captan (3a,4,7,7a-tetrahydro-2-[(trichloromethyl)thio]-1*H*-isoindole-1,3(2*H*)-dione)] to provide protection against the onset of Northern leaf spot symptoms. To further prevent onset of disease symptoms in the yield trials, plots were treated with 0.29 L ha^{-1} of propiconazole (1-[[2-(2,4-dichlorophenyl)-4-propyl-1,3-dioxolan-2-yl]methyl]-1*H*-1,2,4-triazole) beginning when plants were approximately 15 cm in height and continuing until silking. Each location was sprayed three times in 1996 and five times in 1997, except Carroll 1997, which was sprayed only four times. At the Ames location, an application of 1.7 kg ha^{-1} per acre of mancozeb was made after pollination

in 1996, and applications were made after pollination every 6 d in 1997 for 24 d (5 total applications). Two disease ratings were taken at Ames in 1997 for use as covariates in data analysis.

Genetic Model

Harris (1964) extended the classical genetic model first introduced by Fisher (1918) to include inbred relatives. The value of genotype A_iA_j in a population of individuals in Hardy-Weinberg equilibrium is (Fisher, 1918):

$$g_{ij} = \mu + \alpha_i + \alpha_j + \delta_{ij},$$

where g_{ij} = genetic value of genotype A_iA_j, μ = population mean at panmixia, α_i = additive effect of allele A_i, and δ_{ij} = dominance deviation of genotype A_iA_j.

Under this model, the covariance between two individuals, X and Y is:

$$C_{X,Y} = 2\theta_{XY}\sigma_A^2 + 2(\Delta_{\bar{X}+\bar{Y}} - \delta_{\bar{X}\bar{Y}})\sigma_D^2$$
$$+ 2(\gamma_{\bar{X}Y} + \gamma_{X\bar{Y}})D_1 + \delta_{\bar{X}\bar{Y}}D_2^*$$
$$+ (\Delta_{\bar{X}\cdot\bar{Y}} - F_{\bar{X}}F_{\bar{Y}})H^*,$$

where $F_{\bar{X}}$, $F_{\bar{Y}}$, θ_{XY}, $\gamma_{\bar{X}Y}$, $\gamma_{X\bar{Y}}$, $\Delta_{\bar{X}+\bar{Y}}$, $\Delta_{\bar{X}\cdot\bar{Y}}$, and $\delta_{\bar{X}\bar{Y}}$ are probabilities of identity by descent for sets of two, three, or four alleles (Cockerham, 1971; Harris, 1964), and

$$\sigma_A^2 = \sum_i p_i\alpha_i^2 = \text{additive variance,}$$

$$\sigma_D^2 = \sum_i\sum_j p_ip_j\delta_{ij}^2 = \text{dominance variance,}$$

$$D_1 = \sum_i p_i\alpha_i\delta_{ii} = \text{covariance between additive effects}$$

and homozygous dominance effects,

$$D_2^* = \sum_i p_i\delta_{ii}^2 - \left(\sum_i p_i\delta_{ii}\right)^2 = \text{variance of homozygous}$$

dominance deviations,

and

$$H^* = \left(\sum_i p_i\delta_{ii}\right)^2 = \text{sum of homozygous dominance}$$

deviations, squared.

Variances of Effects of Individuals

Our objectives were to quantify quantitative genetic effects of individuals in the BS13(S)C0 population. As such, terms in the genetic model must be related to individuals (Table 1).

Table 1. Model expressions, Expectations [E(·)], variances [V(·)], and covariances [C(·)] for genotypic values (G), breeding values (A), and dominance deviations (D) of noninbred ($F = 0$) and inbred ($F = 1$) individuals.

Value	Noninbred	Inbred
G	$\alpha_i + \alpha_j + \delta_{ij}$	$2\alpha_i + \delta_{ii}$
A	$\alpha_i + \alpha_j$	$2\alpha_i$
D	δ_{ij}	δ_{ii}
E(G)	0	$\sum_i p_i\delta_{ii}$
E(A)	0	0
E(D)	0	$\sum_i p_i\delta_{ii}$
V(G)	$\sigma_A^2 + \sigma_D^2$	$2\sigma_A^2 + 4D_1 + D_2^*$
V(A)	σ_A^2	$2\sigma_A^2$
V(D)	σ_D^2	D_2^*
C(G,A)	σ_A^2	$2(\sigma_A^2 + D_1)$
C(G,D)	σ_D^2	$2D_1 + D_2^*$
C(A,D)	0	$2D_1$

Genetic effects of individuals are their genotypic values, G, expressed as deviations from the population mean, which can be decomposed into breeding values, A, and dominance deviations, D. Falconer and Mackay (1996) define the breeding value, A, of an individual as "twice the mean deviation of the progeny from the population mean" (p. 114) and the dominance deviation, D, as "the difference between the genotypic value G and breeding value A of a particular genotype" (p. 116). Individual effects, G, A, and D, are defined with respect to a panmictic reference population, therefore, their definitions remain independent of an individuals inbreeding coefficient: (i) the genotypic value, G, is defined as a deviation from the panmictic population mean, (ii) the breeding value is defined as twice the deviation from the panmictic population mean of a random sample of offspring derived from mating the individual to individuals randomly sampled from the panmictic reference population, and (iii) the dominance deviation is a contrast between the genotypic value and the breeding value, both defined with respect to the panmictic reference population. The expected breeding value of a randomly sampled individual is always zero (Table 1). In contrast to breeding values, the expected value of the genotypic value (G) and dominance deviation (D) of a randomly sampled individual is a function of the individual's inbreeding coefficient, F, namely,

$$F\sum_i p_i\delta_{ii}.$$

The expression

$$\sum_i p_i\delta_{ii}$$

is the single-locus expectation of average inbreeding depression. Variances of genotypic values, breeding values, and dominance deviations are functions of the inbreeding coefficient as well (Table 1). Variance of breeding values is always a function of the additive genetic variance, σ_A^2, whereas the variance of dominance deviations is σ_D^2 in noninbred individuals ($F = 0$) and D_2^* in inbred individuals ($F = 1$) (Table 1). Additional variances and covariance for noninbred and inbred individuals are provided in Table 1. In summary, definitions of values of individuals (G, A, and D) do not depend on an individuals inbreeding coefficient, whereas their quantitative genetic properties, namely expected values and variances, are affected by the level of inbreeding of an individual, a point central to the arguments made in this report.

Estimator of the Average Degree of Dominance

The average degree of dominance of genes controlling quantitative traits can be estimated in a population with two equally frequent alleles by means of a ratio of dominance and additive genetic variances,

$$\bar{d} = \sqrt{\frac{2\sigma_D^2}{\sigma_A^2}}$$

(Comstock and Robinson, 1948). The estimator of Comstock and Robinson (1948) cannot be applied unless prior information is available that allelic frequencies at segregating loci are equal to 0.5 in the reference population, as in an F_2 population derived from a cross between two inbred lines. In a randomly mating population, randomly chosen individuals may be self-pollinated to obtain subpopulations that are genetically analogous to biparental F_2 populations; in these subpopulations allelic frequencies are 0.5 for loci that were heterozygous in the self-pollinated subpopulation founders. Therefore, Comstock and Robinson's (1948) estimator could be applied to individual subpopulations derived by self-pollinating individuals in any type of reference population. However, analysis of a single

subpopulation would not be representative of the reference population, so an estimator is desired that can be pooled across a large sample of subpopulations derived from a common reference population. An alternative to estimating σ_A^2 and σ_D^2 explicitly in a large number of subpopulations would be to predict expected values of σ_A^2 and σ_D^2 within subpopulations from parameters measured in the base population. Cockerham (1984) and Jiang and Cockerham (1990) developed expressions to predict the expected additive variance, σ_{A*}^2, and dominance variance, σ_{D*}^2, that would be observed within subpopulations derived from a common base population: $\sigma_{A*}^2 = (1 - \theta)\sigma_A^2 + 2(\theta - \gamma - 2\Delta + 2\delta)\sigma_D^2 + 4(\theta - \gamma)D_1 + 2(\gamma - \delta)D_2^* + 2(\gamma - \Delta)H^*$ and $\sigma_{D*}^2 = (1 - 3\theta + 2\gamma + 2\Delta - 2\delta)\sigma_D^2 + (\theta - 2\gamma + \delta)D_2^* + (\theta - 2\gamma + \Delta)H^*$.

Following methods used in Cockerham (1983), the following descent measures were obtained between individuals within subpopulations derived by self-pollination of a single individual:

$$\theta = \tfrac{1}{2}(1 + F),$$
$$\gamma = \Delta = \tfrac{1}{4}(1 + 3F),$$
$$\delta = \tfrac{1}{8}(1 + 7F),$$

where F = inbreeding coefficient of the subpopulation founder.

Substituting expected additive variance, σ_{A*}^2, and dominance variance, σ_{D*}^2, within two-allele subpopulations derived from the base population yields the following unbiased estimator, which is applicable to any reference population:

$$\bar{d} = \sqrt{\frac{2\sigma_{D*}^2}{\sigma_{A*}^2}} = \sqrt{\frac{\sigma_D^2 + \tfrac{1}{2}D_2^* + H^*}{\sigma_A^2 + 2D_1 + \tfrac{1}{2}D_2^*}}.$$

In a reference population with two equally frequent alleles per locus, $D_1 = D_2^* = 0$, and $H^* = \sigma_D^2$ (Cockerham, 1984) so that our estimator,

$$\bar{d} = \sqrt{\frac{\sigma_D^2 + \tfrac{1}{2}D_2^* + H^*}{\sigma_A^2 + 2D_1 + \tfrac{1}{2}D_2^*}},$$

reduces to Comstock and Robinson's (1948) estimator for a biparental population,

$$\bar{d} = \sqrt{\frac{2\sigma_D^2}{\sigma_A^2}}.$$

Data Analysis

Data were analyzed by fitting a mixed linear model of the form: $\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{e}$ where,

$\boldsymbol{\beta}$ = vector of fixed effects,

$\mathbf{u}$ = vector of random effects,

$\mathbf{e}$ = vector of residuals,

$\mathbf{X}$ = incidence matrix relating observations

    to fixed effects, and

$\mathbf{Z}$ = incidence matrix relating observations

    to random effects.

Fixed effects were included for environments (location–year combinations), whole-plot blocks, lattice rows for all traits, lattice columns for days to mid pollen and mid silk, and covariates. Environments and blocks were considered fixed because they were not variables of primary interest in our study. Stand density of individual plots was fit as a covariate when significant at $P \le 0.05$. Northern leaf spot ratings were fit as covariates for the Ames, 1997 location, and the genotype of the

family (resistant, segregating, susceptible) was fit for grain moisture in three of the environments.

The vector of random effects, $\mathbf{u}$, had the form $\mathbf{u}' = (\mathbf{u}_{1,1} \cdots \mathbf{u}_{i,j} \cdots \mathbf{u}_{200,5})$, where $\mathbf{u}_{i,j}$ is a random vector for the ith line ($i = 1..200$) in the jth environment ($j = 1..5$). Vectors $\mathbf{u}_{i,j}$ had the form $\mathbf{u}_{i,j}' = (u_1 \cdots u_k \cdots u_5)$, where u_k is a random line effect for the ith line in the jth environment for the kth generation of inbreeding ($k = 1..5$). The 200 lines were considered independent subjects in the mixed model because each was derived from an independent founder individual in the base population. The variance of the random vectors $\mathbf{u}_{i,j}$ was $Var(\mathbf{u}_{i,j}) = \mathbf{A}_1\sigma_A^2 + \mathbf{A}_2\sigma_D^2 + \mathbf{A}_3D_1 + \mathbf{A}_4D_2^* + \mathbf{A}_5H^* + \mathbf{A}_1\sigma_{AE}^2 + \mathbf{A}_2\sigma_{DE}^2 + \mathbf{A}_3D_{1E} + \mathbf{A}_4D_{2E}^* + \mathbf{A}_5H_E^*$. The covariance between random vectors $\mathbf{u}_{i,j}$ and $\mathbf{u}_{i,j'}$, representing the same line grown in different environments, was $Cov(\mathbf{u}_{i,j}, \mathbf{u}_{i,j'}) = \mathbf{A}_1\sigma_A^2 + \mathbf{A}_2\sigma_D^2 + \mathbf{A}_3D_1 + \mathbf{A}_4D_2^* + \mathbf{A}_5H^*$. The covariances between $\mathbf{u}_{i,j}$ and $\mathbf{u}_{i'j}$ or $\mathbf{u}_{i'j'}$, representing different lines grown in the same or in different environments, respectively, were zero because all lines were derived from independent founders in the base population.

Matrices $\mathbf{A}_1 \cdots \mathbf{A}_5$ were matrices of coefficients describing the expected genotypic variance of the random vector of line effects for the five generations of inbreeding. Coefficients were obtained from probabilities of identity by descent obtained for the five generations of inbreeding following Cockerham (1971, 1983) and are given in Table 2. The components σ_{AE}^2, σ_{DE}^2, D_{1E}, D_{2E}^*, and H_E^* are the variances and covariances of common environment effects which describe the effects of environments shared by genotypes grown in a common environment. These components are the mixed linear model equivalents of genotype x environment interaction in analysis-of-variance models. Error variances were found to be heterogeneous by environment and inbreeding level, and were estimated as such in the mixed model.

All independent variables, fixed and random, were simultaneously fit in a mixed linear model (Henderson, 1984). Restricted Maximum Likelihood (REML) estimators of genetic variances were obtained by solving the REML equations (Searle et al., 1992) by means of Newton Raphson iteration. All calculations were carried out by the mixed procedure in SAS Version 6 (SAS Institute, 1996). Asymptotic variances and covariances of the variance component estimates were obtained from two times the inverse of the matrix of second derivatives of the restricted likelihood function with respect to the variance components (SAS Institute, 1996). Exact confidence limits were not available for variance components because their exact sampling distributions are unknown. Therefore, we relied on asymptotic normality and assumed any component larger than two standard errors was significantly different from zero at $P \le 0.05$. Variances of genotypic values, breeding values, and dominance deviations were estimated as linear functions of

Table 2. Coefficients for genotypic covariance components in the 15 covariance expressions relating five generations of inbreeding.

(Co)variance	Component				
	σ_A^2	σ_D^2	D_1	D_2^*	H^*
$V(S_0)$	0.250	0.000	0.000	0.000	0.000
$Cov(S_0,S_1)$	0.500	0.000	0.250	0.000	0.000
$V(S_1)$	1.000	0.250	1.000	0.125	0.000
$Cov(S_0,S_2)$	0.500	0.000	0.375	0.000	0.000
$Cov(S_1,S_2)$	1.000	0.125	1.250	0.188	0.000
$V(S_2)$	1.500	0.125	2.500	0.563	0.063
$Cov(S_0,S_3)$	0.500	0.000	0.438	0.000	0.000
$Cov(S_1,S_3)$	1.000	0.063	1.375	0.219	0.000
$Cov(S_2,S_3)$	1.500	0.063	2.625	0.594	0.031
$V(S_3)$	1.750	0.063	3.250	0.781	0.047
$Cov(S_0,S_4)$	0.500	0.000	0.469	0.000	0.000
$Cov(S_1,S_4)$	1.000	0.031	1.438	0.234	0.000
$Cov(S_2,S_4)$	1.500	0.031	2.688	0.609	0.016
$Cov(S_3,S_4)$	1.750	0.031	3.313	0.797	0.023
$V(S_4)$	1.875	0.031	3.625	0.891	0.027

the REML estimates of the genotypic covariance components and their standard errors were obtained from the asymptotic variance-covariance matrix of covariance parameter estimates. Genetic variance component ratios and the average degree of dominance, $\bar{d}$, were estimated and approximate standard errors derived by a first order Taylor series approximation as described in Casella and Berger (1990). We used the degree of dominance estimator that we have shown to be unbiased by variation in allelic frequencies as opposed to the classical estimator of Comstock and Robinson (1948) that is biased if frequencies of segregating alleles differ from 0.5. Correlations between effects of individuals, G, A, and D for inbred individuals were computed as:

$$r_{G,A} = \frac{2(\sigma_A^2 + D_1)}{\sqrt{2\sigma_A^2(2\sigma_A^2 + 4D_1 + D_2^*)}},$$

$$r_{G,D} = \frac{2D_1 + D_2^*}{\sqrt{D_2^*(2\sigma_A^2 + 4D_1 + D_2^*)}},$$

and

$$r_{A,D} = \frac{2D_1}{\sqrt{2\sigma_A^2 D_2^*}}.$$

These values are consistent with expressions given by Corne-lius (1988). For noninbred individuals, A and D are independent, and the correlations between G and A and D were computed as:

$$r_{G,A} = \frac{\sigma_A^2}{\sqrt{\sigma_A^2(\sigma_A^2 + \sigma_D^2)}}$$

and

$$r_{G,D} = \frac{\sigma_D^2}{\sqrt{\sigma_D^2(\sigma_A^2 + \sigma_D^2)}}.$$

Least squares means were obtained for each whole plot (replicate-inbreeding level combination) from the mixed model and used as individual observations in an analysis of variance to test and estimate inbreeding depression rates. Environments and replicates within environments were fit as fixed effects. Inbreeding depression rates and their interactions with environments were added to the model in stepwise fashion, and the reduction in sums of squares due to addition of the effect was used as a numerator in the F-test with the residual error as the denominator. Linear and quadratic inbreeding depression rates were added first to the model, then their interactions with environments. Identical procedures were used to analyze the bulk entry experiment, except that individual plot observations were fit in the model instead of least squares estimates

Table 3. S_0 generation means, inbreeding depression, and regression coefficients for the combined analyses across five environments for two experiments.

Effect	Individual lines[†]			Bulks[‡]		
	Estimate	Lower bound§	Upper bound	Estimate	Lower bound	Upper bound
	Grain yield (Mg ha^{-1})					
S_0 mean¶	5.07	4.95	5.18	5.24	4.90	5.57
Inbreeding depression††	2.37	2.52	2.22	2.27	2.64	1.90
Linear regression‡‡	1.06	1.61	0.51	0.90	2.28	−0.48
Quadratic regression	1.30	1.87	0.74	1.36	2.89	−0.16
Percent inbreeding depression§§	47	51	43	43	54	34
	Grain Moisture (g hg^{-1})					
S_0 mean	24.64	24.34	24.93	23.71	23.34	24.08
Inbreeding depression	1.17	1.59	0.76	1.00	1.58	0.42
	Ear height (cm)					
S_0 mean	108.6	106.4	110.7	105.0	103.3	106.7
Inbreeding depression	27.7	30.7	24.7	22.4	25.1	19.7
Percent inbreeding depression	25	29	22	21	24	18
	Plant height (cm)					
S_0 mean	220.4	217.7	223.1	217.0	215.0	218.9
Inbreeding depression	45.9	49.8	42.0	36.3	39.3	33.3
Percent inbreeding depression	21	23	19	17	18	15
	Days to mid pollen (days after June 30)					
S_0 mean	28.4	27.9	28.9	29.2	28.6	29.8
Inbreeding depression	−2.8	−2.3	−3.4	−2.5	−1.9	−3.1
Linear regression	−0.1	2.0	−2.2	NS	NS	NS
Quadratic regression	−2.7	−0.6	−4.8	NS	NS	NS
	Days to mid silk (days after June 30)					
S_0 mean	30.6	29.9	31.3	31.5	30.9	32.1
Inbreeding depression	−3.1	−2.2	−3.9	−2.7	−2.1	−3.3
Linear regression	0.6	3.6	−2.4	NS	NS	NS
Quadratic regression	−3.7	−0.6	−6.7	NS	NS	NS

† Data from evaluation of individual lines.
‡ Data from evaluation of balanced bulks of lines.
§ Lower and upper bounds of a 95% confidence interval.
¶ Mean performance of the population at $F = 0$.
†† Total inbreeding depression computed as the predicted difference between noninbred ($F = 0$) and inbred ($F = 1$) generations.
‡‡ Linear regression and quadratic regression coefficients are the results of regressing population means on the inbreeding coefficient. Individual regression coefficients are given only if the quadratic coefficient was significant at $P \leq 0.05$. If the quadratic regression coefficient was not significant, it was dropped from the model, and total inbreeding depression is equivalent to the linear regression coefficient on F. Regression coefficients were multiplied by −1 to express decreases in value as positive values of inbreeding depression and increases in value as negative inbreeding depression consistently with the literature (Falconer and MacKay, 1996).
§§ Percent inbreeding depression was calculated as 100 times total inbreeding depression divided by the S_0 population mean.
NS Quadratic regression coefficient was not significant at $P \leq 0.05$ so that inbreeding depression was equivalent to the linear regression coefficient.

of block effects. Order in which effects were added to the model did not affect significance. If inbreeding depression rates differed significantly among environments, regressions for single environments were examined. Upper and lower bounds of 95% confidence limits were computed for panmictic population means and inbreeding depression rates by means of the residual error mean-square and appropriate values from the t-distribution.

RESULTS

Inbreeding Depression

Inbreeding depression was found for all six traits in both the evaluation of individual lines and in the bulk entry experiment (Table 3). Differences in inbreeding depression rates among environments were found for grain yield, grain moisture, and days to mid pollen in both experiments and for ear height in the evaluation of individual lines (Fig. 1, data not shown for grain moisture, ear height, and days to mid pollen). Nonlinear inbreeding depression rates, i.e., significant quadratic regression coefficients, were found for grain yield in both experiments and flowering dates in the evaluation of individual lines (Table 3). Although none of the differences was significant, there was a trend for slightly less inbreeding depression in the bulk entry experiment. Precision of inbreeding depression rates was generally similar between experiments except for grain yield (Table 3). The confidence interval on the rate of inbreeding depression for grain yield in the evaluation of individual lines was less than half the size of the corresponding interval from the bulk entry experiment (Table 3).

Genetic Variances

All five genotypic covariance components (σ_A^2, σ_D^2, D_1, D_2^*, H^*) were larger than two standard errors for
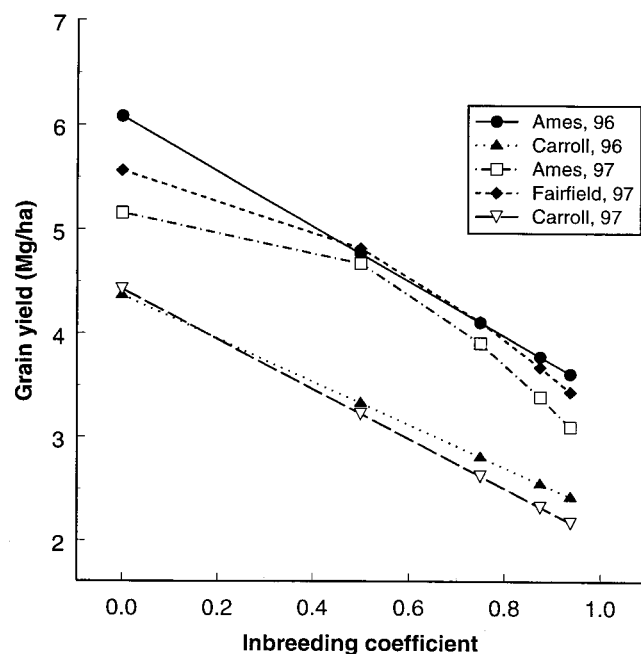

Fig. 1. Regressions of mean grain yield on the pedigree inbreeding coefficient for each of five environments from the evaluation of individual lines. Quadratic regression coefficients were significant for the Ames 1997 and Fairfield 1997 environments.

all traits except D_1 for grain moisture and days to mid pollen and D_2^* for days to mid pollen and days to mid silk. Estimates of the covariance D_1 were negative for every trait (Table 4). All five genotype × environment interaction components were significant for grain yield. For other traits, genotype × environment interactions were generally small with respect to main effects, and usually not larger than two standard errors except σ_{AE}^2 and D_{2E}^* for grain moisture and H_E^* for ear height (Table 4). Predicted variances among lines in each generation of inbreeding showed an increasing trend from the S_0 (noninbred half-sib families) generation to the S_4 generation (Table 4). The predicted variance among S_4 lines ($F = 0.9375$) corresponded closely for every trait to the predicted variance among inbred genotypic values (Table 4).

The ratio D_2^*/σ_D^2 was less than one for days to mid pollen, greater than one for grain moisture, greater than two for grain yield and days to mid silk, and greater than three for ear height and plant height (Table 4). Under a purely additive genetic model, the variance of genotypic values, G, doubles upon inbreeding individuals from $F = 0$ to $F = 1$. The ratio of total genetic variance at $F = 1$ to total variance at $F = 0$, $(2\sigma_A^2 + 4D_1 + D_2^*/(\sigma_A^2 + \sigma_D^2)$, was 1.71 for grain moisture, and between 0.95 and 1.18 for remaining traits, demonstrating that inbreeding did not result in a doubling of total genetic variance as expected under an additive model (Table 4). The ratio of total genetic variance at $F = 1$ to additive variance, also expected to be 2 under an additive model, was 2.39 and 2.28 for grain yield and grain moisture, respectively and was less than two for other traits (Table 4). In contrast to changes in total variance, large increases in variance of dominance deviations were observed with inbreeding. The variance of dominance deviations of inbred individuals, D_2^*, was 2.65, 3.33, and 3.01 times the variance of dominance deviations of noninbred individuals, σ_D^2, for grain yield, ear height, and plant height, respectively.

Estimates of the degree of dominance were over 2 for all traits except grain moisture (Table 4). The degree of dominance for grain moisture was not significantly greater than 1.0, which corresponds to complete dominance (Table 4). Correlations between genotypic values, G, and breeding values, A, ranged from 0.48 to 0.80 for noninbred progeny and from 0.34 to 0.93 for inbred progeny (Table 5). The correlation between G and D was in general much lower than the correlation between G and A for both inbred and noninbred progeny, except in the case of grain yield. Grain yield was unique in that the correlation between G and D was similar to the correlation between G and A in noninbred progeny, and was greater than the correlation between G and A in inbred progeny (Table 4).

DISCUSSION

Inbreeding Depression

As with previous studies in maize, we found significant inbreeding depression for all traits studied. How-

Table 4. Estimates of genetic variances, variance component ratios, and degree of dominance expressed with standard errors for six traits in the BS13(S)C0 population grown at two locations in 1996 and three locations in 1997.

| Component | Genetic variances | | | | | |
	Grain yield Mg^2 ha^{-2}	Grain moisture g^2 ka^{-2}	Ear height cm^2	Plant height cm^2	Days to mid-pollen days^2	Days to mid-silk days^2
σ_A^2	0.29 ± 0.05	5.2 ± 0.6	149 ± 17	208 ± 23	2.1 ± 0.3	4.1 ± 0.5
σ_D^2	0.32 ± 0.09	1.7 ± 0.7	44 ± 14	64 ± 21	1.0 ± 0.4	1.0 ± 0.4
D_1	-0.18 ± 0.06	-0.4 ± 0.4	-66 ± 13	-76 ± 18	-0.3 ± 0.3	-1.0 ± 0.4
D_2^*	0.85 ± 1.09	2.9 ± 1.2	147 ± 33	194 ± 47	0.6 ± 0.7	1.7 ± 1.0
H^*	1.55 ± 0.48	6.5 ± 4.8	344 ± 89	661 ± 149	6.4 ± 2.1	21.0 ± 4.2
σ_{AE}^2	0.12 ± 0.04	1.0 ± 0.2	4 ± 3	7 ± 5	0.2 ± 0.1	0.2 ± 0.1
σ_{DE}^2	0.11 ± 0.06	0.1 ± 0.5	2 ± 6	9 ± 9	-0.4 ± 0.2	-0.5 ± 0.2
D_{1E}	-0.11 ± 0.04	-0.5 ± 0.3	-1 ± 4	0 ± 6	-0.1 ± 0.2	-0.2 ± 0.2
D_{2E}^*	0.33 ± 0.11	2.2 ± 0.8	1 ± 10	3 ± 15	0.4 ± 0.4	0.8 ± 0.5
H_E^*	0.54 ± 0.29	4.6 ± 3.2	115 ± 31	128 ± 45	-0.3 ± 1.2	0.3 ± 1.7
	Variances of genotypic values, G, of noninbred and inbred individuals					
Noninbred	0.61 ± 0.10	6.9 ± 0.9	194 ± 22	272 ± 32	3.0 ± 0.5	5.1 ± 0.7
Inbred	0.69 ± 0.09	11.7 ± 1.2	183 ± 19	307 ± 33	3.6 ± 0.4	6.0 ± 0.7
	Predicted variances of observed generations of inbreeding					
$V(S_0)$	0.07 ± 0.01	1.3 ± 0.2	37 ± 4	52 ± 6	0.5 ± 0.1	1.0 ± 0.1
$V(S_1)$	0.29 ± 0.03	5.6 ± 0.5	113 ± 11	172 ± 16	2.1 ± 0.2	3.6 ± 0.4
$V(S_2)$	0.59 ± 0.04	9.1 ± 0.7	170 ± 11	281 ± 19	3.3 ± 0.2	6.1 ± 0.4
$V(S_3)$	0.67 ± 0.06	10.5 ± 0.9	182 ± 14	304 ± 24	3.5 ± 0.3	6.4 ± 0.5
$V(S_4)$	0.69 ± 0.07	11.2 ± 1.0	184 ± 17	308 ± 28	3.6 ± 0.4	6.3 ± 0.6
	Covariances between effects of individuals					
Cov(G,A)	0.21 ± 0.08	9.6 ± 1.1	167 ± 23	264 ± 34	3.6 ± 0.5	6.3 ± 0.7
Cov(G,D)	0.48 ± 0.11	2.1 ± 1.1	16 ± 22	42 ± 33	0.0 ± 0.4	-0.3 ± 0.7
Cov(A,D)	-0.36 ± 0.12	-0.7 ± 0.9	-131 ± 26	-151 ± 36	-0.6 ± 0.5	-1.9 ± 0.7
	Variance ratios and average degree of dominance ($\bar{d}$)†					
$(2\sigma_A^2 + 4D_1 + D_2^*)/(\sigma_A^2 + \sigma_D^2)$	1.14 ± 0.26	1.71 ± 0.30	0.95 ± 0.15	1.13 ± 0.18	1.18 ± 0.24	1.17 ± 0.21
$(2\sigma_A^2 + 4D_1 + D_2^*)/\sigma_A^2$	2.39 ± 0.85	2.28 ± 0.53	1.23 ± 0.28	1.48 ± 0.34	1.73 ± 0.50	1.47 ± 0.36
D_2^*/σ_D^2	2.65 ± 0.96	1.70 ± 1.18	3.33 ± 1.43	3.01 ± 1.36	0.62 ± 0.75	1.62 ± 1.25
$\bar{d}$	2.57 ± 0.43	1.28 ± 0.39	2.24 ± 0.34	2.32 ± 0.34	2.06 ± 0.41	2.76 ± 0.42

† Variance ratios and degree of dominance are unitless.

ever, we also found evidence for nonlinear inbreeding depression for three traits, a result not obtained in many previous studies, including past work in Iowa Stiff Stalk Synthetic populations. Crow and Kimura (1970, p. 81) point out that nonlinear inbreeding depression can result from dominant × dominant epistatic interactions. In our experiment, inbreeding depression rates increased as the inbreeding coefficient increased, corresponding to reinforcing epistasis, a situation in which "the deleterious effect of two loci is more than cumulative" (Crow and Kimura, 1970, p. 80). Another possible explanation for nonlinear inbreeding depression could be pleiotropy with Northern leaf spot symptoms in our experiment, as we observed the disease in every environment. However, nonlinear inbreeding depression was also found for flowering dates, traits that were unaffected by this disease because symptoms were not observed until after

flowering. In addition, detection of nonlinear inbreeding depression in different environments did not coincide with variation in disease severity among environments.

Variance Component Estimation Issues

Wright and Cockerham (1986) showed that with relatives derived exclusively by self-pollination, breeding values and panmictic dominance deviations are completely confounded. As a result, σ_A^2 and σ_D^2 are separately unestimable. Similar problems exist in any pedigrees containing few outbred progeny, i.e., breeding values and dominance deviations are partially or completely confounded (Cockerham, 1983; Wright and Cockerham 1986; Cornelius and Van Sanford, 1988; Cornelius, 1988). Cornelius and Van Sanford (1988) suggested outcrossing S_0 plants (individuals used as founders of inbred lines) to produce full-sib families to estimate the quantity $\frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_D^2$. Cockerham (1983) pointed out that with self-pollination, progenies are needed from early in the inbreeding process to obtain information on the dominance variance. We utilized both suggestions: (i) we produced the equivalent of half-sib families on our S_0 plants to produce a clean estimate of σ_A^2, and (ii) we included all of the earliest generations of inbreeding to provide the maximal amount of information on σ_D^2. Although we reduced correlations between estimates of σ_A^2 and σ_D^2, we did find high correlations between estimates of σ_A^2 and D_1, and between estimates of D_1 and D_2^*. As an example, following is the

Table 5. Correlations between genotypic values of individuals, their breeding values and their dominance deviations for noninbred and inbred individuals. Breeding values and dominance deviations are independent by definition in noninbred individuals.

| Trait | Noninbred individuals | | Inbred individuals | | |
	G,A	G,D	G,A	G,D	A,D
Grain yield	0.48	0.52	0.34	0.63	−0.52
Grain moisture	0.75	0.25	0.87	0.37	−0.13
Ear height	0.77	0.23	0.72	0.10	−0.63
Plant height	0.76	0.24	0.74	0.17	−0.53
Mid pollen	0.68	0.32	0.93	0.01	−0.37
Mid silk	0.80	0.20	0.89	−0.08	−0.52

correlation matrix of variance component estimates for grain yield:

$$corr\begin{pmatrix} \hat{\sigma}_A^2 \\ \hat{\sigma}_D^2 \\ \hat{D}_1 \\ \hat{D}_2 \\ \hat{H} \end{pmatrix} = \begin{bmatrix} 1 & -0.03 & -0.74 & 0.44 & -0.08 \\ -0.03 & 1 & -0.08 & -0.01 & -0.09 \\ -0.74 & -0.08 & 1 & -0.84 & 0.15 \\ 0.44 & -0.01 & -0.84 & 1 & -0.39 \\ -0.08 & -0.09 & 0.15 & -0.39 & 1 \end{bmatrix}$$

The failure of our design to reduce correlations between estimates of D_1 and other components was a direct outcome of the inability of our design to resolve breeding values and homozygous dominance deviations. Our design could resolve breeding values and panmictic dominance deviations because we had half-sib families produced on the noninbred founders as well as S_1 lines from the same individuals. However, we did not include outbred progeny of any *inbred* generations, and hence we could not directly estimate breeding values of any inbred generations. Only genotypic values of inbred generations were directly estimable, and as a result, breeding values and dominance deviations of inbred generations were highly correlated within the set of relatives we observed. It appears that the best resolution of all genetic effects, and hence all variance components, requires observing noninbred and inbred generations, as well as outbred progeny (half-sib families for example) of both noninbred and inbred generations. Previous studies of genotypic covariance estimation for inbred relatives (Cockerham,1983; Cornelius, 1988; Cornelius and Van Sanford, 1988; Wright and Cockerham 1986) have resulted in great advances in our ability to apply and interpret the extensions of genotypic covariance theory to inbred relatives put forth by Dewey Harris (1964). However, development of optimal designs for parameter estimation continues to be a work in progress.

Inference Space of Covariance Models—Genes vs. Individuals

The classical linear model of quantitative traits, $g_{ij} = \alpha_i + \alpha_j + \delta_{ij}$ (Fisher, 1918) was derived as a model of the value of a genotype at a single locus. In contrast to single loci, the observational units of quantitative genetics experiments are individuals or families of individuals. As such, estimated components of the linear genetic model reflect genotypic values, breeding values, and dominance deviations of individuals, not single loci. Included in the effects of individuals are not only independent effects of individual loci, but also combined effects of multiple loci such as epistatic interactions and linkage disequilibrium. Design III experiments in maize conducted to estimate the average degree of dominance clearly established the effects of negative linkage disequilibria on estimates of variance components, particularly dominance variance, σ_D^2 (Gardner and Lonnquist, 1959; Moll et al., 1964; Han and Hallauer, 1989). These classical studies used design III mating designs (Comstock and Robinson, 1948) to estimate the average degree of dominance both in F_2 populations and in random mated synthetics derived from the same F_2 populations.

Estimates of dominance variance, σ_D^2, were reduced in nearly every case by random mating of F_2 populations, which resulted in reduced estimates of the average degree of dominance. It was concluded that repulsion phase linkages had caused expression of apparent overdominance, upwardly biasing estimates of the average degree of dominance and of dominance variance in the nonrandom mated F_2 populations. Although the conclusion was reached that estimates of σ_D^2 in the original F_2 populations were biased by linkage disequilibrium, they were still reported as estimates of dominance variance, despite the fact that the authors had clearly established a violation of the assumption of no linkage disequilibrium. More recent theoretical work on additive $\times$ additive epistatic effects has established that much of the variability attributable to additive by additive epistasis is directly confounded with additive effects in a way that additive $\times$ additive epistasis contributes directly to additive genetic variance (Cheverud and Routman, 1995, 1996; Goodnight, 1987, 1988). Assuming that linkage disequilibrium and epistasis are not present would be unreasonable in any setting. Rather than make such assumptions, it seems more reasonable to interpret genotypic variance component estimates under the assumption that they are estimates of the proportion of genetic variance describable by single-locus or marginal effects, with the caveat that an unknown proportion of variance described by single-locus genetic component estimates is due to linkage disequilibrium and or epistasis. As such, we have focused our interpretations not on additive and/or dominance effects of individual genetic loci or individual genes, but rather on average additive effects, i.e., breeding values, and on average dominance deviations observed in *individuals*. Averages of breeding values and dominance deviations for individuals include the marginal effects ascribable to single-locus genetic effects plus unestimable biases due to epistatic interactions and linkage disequilibrium.

Inbred vs. Noninbred Dominance Deviations

Dominance deviations are defined as contrasts between the genotypic value of an individual and its breeding value, independent of the level of inbreeding. However, expected values of dominance deviations differ between inbred and noninbred individuals. Dominance deviations at $F = 0$, δ_{ij}, have expected value of zero, variance σ_D^2, and are independent of breeding values (zero covariance). Dominance deviations at $F = 1$, δ_{ii}, [referred to by Cornelius (1988) as "within-locus inbreeding depression effects"] have a nonzero expectation of

$$h = \sum_i p_i \delta_{ii},$$

variance D_2^*, and a covariance with breeding values of $2D_1$ (Table 1). Therefore, the quantitative genetic properties of dominance deviations change with the inbreeding level of individuals although the way they are estimated does not. The maize quantitative genetics literature in particular contains numerous estimates of the domi-

nance variance; Hallauer and Miranda (1988) summarized estimates of additive and dominance variance from 99 independent studies in maize. However, prior to our work, only one study in the maize literature provided estimates of D_2^* (Cornelius, 1988; Cornelius and Dudley, 1976). Given the ubiquitous nature of inbreeding depression in maize and the economic importance of the hybrid maize industry, a clear need exists for a better understanding of dominance deviations of inbred individuals. Dominance deviations of inbred individuals are the quantitative genetic basis (under a single-locus model) for inbreeding depression, i.e., the average inbreeding depression in a population has an expected value of

$$\sum_i p_i \delta_{ii},$$

which is identical to the expected value of dominance deviations of inbred individuals. The importance of understanding dominance deviations of inbred individuals is further highlighted by the fact that we found the variance of dominance deviations of inbred individuals was 2.65, 3.33, and 3.01 times the variance of dominance deviations of noninbred individuals for grain yield, ear height, and plant height.

Covariance between Breeding Values and Dominance Deviations in Inbred Individuals

Variances of breeding values and dominance deviations both increased with inbreeding: (i) variance of breeding values of inbred individuals is twice the variance of breeding values of noninbred individuals by definition, (ii) variance of inbred dominance deviations was greater than the variance of panmictic dominance deviations for five of six traits (Table 4). However, the variance of the sum of breeding values and dominance deviations, the genotypic value, changed very little with inbreeding (Table 4). The result was a negative covariance between breeding values and dominance deviations of inbred individuals, $2D_1$, for all six traits we studied (Table 4). Hence, one of the outcomes of negative correlation between breeding values and inbred dominance deviations is a lower variance among genotypic values of inbred individuals than would be observed if breeding values and inbred dominance deviations were independent. Negative correlation between breeding values and inbred dominance deviations was consistent with previous reports of Coors (1988), Cornelius (1988), and Shaw et al. (1998). In addition, Shaw et al. (1998) also found that dominance deviations tended to be larger in inbred progeny than in noninbred progeny, as we did.

Degree of Dominance

The average degree of dominance was greater than one, corresponding to overdominance, for all six traits we studied. Previous estimates of the average degree of dominance in maize (see introduction) and estimates of heterozygous effects of mutations in other species (Crow, 1993; Wang et al., 1998) suggest that the degree of dominance is generally in the complete to partial dominant

range. Furthermore, previous work in maize found that estimates of the degree of dominance tended to be upwardly biased by linkage disequilibrium, i.e., pseudo-overdominance. Linkage disequilibrium is increased by finite population size (Bulmer, 1980, p. 226; Hill and Robertson, 1968; Qureshi and Kempthorne, 1968; Tachida and Cockerham, 1989) and selection (Bulmer, 1974; Hill and Robertson, 1968; Hospital and Chevalet, 1996; Qureshi and Kempthorne, 1968; Robertson, 1977). Because of the small population sizes and intense selection found in many synthetic maize populations, linkage disequilibrium, and hence pseudo-overdominance, is to be expected. Therefore, given previous studies, we can speculate that our high estimates of the degree of dominance in BS13(S)C0 were likely due to excess repulsion phase linkages among genes with dominant effects. However, we cannot preclude overdominance on the basis of our data. We also detected large estimates of H^*, which occurs in the numerator of our degree of dominance estimator. Cockerham (1984) pointed out that with two alleles per locus, $H^* = \sigma_D^2$. Comparison of our estimates of H^* with σ_D^2 for these traits suggests that the hypothesis of two alleles per locus is likely unacceptable. Shaw et al. (1998) pointed out that if inbreeding depression results from the effects of many loci H^* would be expected to be small because it is a sum of squared inbreeding depression effects. Conversely, a large H^*, as we obtained, may suggest a few loci with large effects on inbreeding depression, or high levels of linkage disequilibrium so that alleles at sets of linked loci are acting as single loci. Therefore, our large estimates of H^* and the degree of dominance could suggest the presence of a few regions with segregating recessives at several loci tightly linked in repulsion phase with relatively large effects. In this context, the genetic model is interpreted as if alleles are really linkage groups. Given the restrictive assumptions required to extend the inference space of genotypic covariance models to individual loci, our work cannot provide any proof of linked sets of recessive genes in repulsion phase with large effects, but based on our data, this is a very plausible hypothesis and one that should be pursued further.

Implications for Breeding and Selection

The large variability in inbred dominance deviations in this population supports the suggestion made by Pray and Goodnight (1995) that inbreeding depression is a variable and selectable trait. Selection does not act directly on inbreeding depression, but rather it acts directly on genotypic values. Because only a single allele can be passed on in meiosis, only the average values of alleles when combined with other alleles, (breeding values) are heritable. However, because dominance deviations in inbred individuals are associated with a single allele that becomes fixed with inbreeding, selection can affect inbred dominance deviations. Selection acts on inbreeding depression through the correlation between inbred dominance deviations and genotypic values. In the case of grain yield, genotypic values of inbred indi-

viduals and their dominance deviations had a correlation of 0.63 (Table 5). In contrast, ear height and plant height, traits that also show inbreeding depression, had correlations between inbred genotypic values and inbred dominance deviations of just 0.10 and 0.17, respectively (Table 5). Hence, selection based on inbred genotypic value will have little effect on inbreeding depression for ear height or plant height, whereas it will have a larger influence on inbreeding depression for grain yield. The correlation between inbred genotypic value and breeding value was 0.34 for grain yield, but it was 0.72 and 0.74 for ear height and plant height, respectively. Hence, selection based on inbred performance will have little effect on noninbred performance for grain yield but will affect noninbred performance for ear height and plant height. This may explain the lack of response to S_2-progeny recurrent selection for population per se performance for grain yield in the BS13 population, as described by Lamkey (1992).

ACKNOWLEDGMENTS

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